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Impacts of climate change and renewable energy development on habitat of an endemic squirrel, *Xerospermophilus mohavensis*, in the Mojave Desert, USA

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ABSTRACT

Predicting changes in species distributions under a changing climate is becoming widespread with the use of species distribution models (SDMs). The resulting predictions of future potential habitat can be cast in light of planned land use changes, such as urban expansion and energy development to identify areas with potential conflict. However, SDMs rarely incorporate an understanding of dispersal capacity, and therefore assume unlimited dispersal in potential range shifts under uncertain climate futures. We use SDMs to predict future distributions of the Mojave ground squirrel, *Xerospermophilus mohavensis* Merriam, and incorporate partial dispersal models informed by field data on juvenile dispersal to assess projected impact of climate change and energy development on future distributions of *X. mohavensis*. Our models predict loss of extant habitat, but also concurrent gains of new habitat under two scenarios of future climate change. Under the B1 emissions scenario- a storyline describing a convergent world with emphasis on curbing greenhouse gas emissions- our models predicted losses of up to 64% of extant habitat by 2080, while under the increased greenhouse gas emissions of the A2 scenario, we suggest losses of 56%. New potential habitat may become available to *X. mohavensis*, thereby offsetting as much as 6330 km^2 (50%) of the current habitat lost. Habitat lost due to planned energy development was marginal compared to habitat lost from changing climates, but disproportionately affected current habitat. Future areas of overlap in potential habitat between the two climate change scenarios are identified and discussed in context of proposed energy development.

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1. Introduction

Many studies modeling the consequences of 20th–21st century climate change on species distributions suggest that the distributions of many North American flora and fauna will be reduced, altered, or eliminated if regional climate trends continue (Rosenzweig et al., 2008, Pearson et al., 2014). Changes in temperature and precipitation are likely to push some ecosystems and their species poleward or up-slope (Hickling et al., 2005, Lenoir et al., 2008), downslope (Serra-Diaz et al., 2014), cause heterogeneous range shifts (Tingley et al., 2012, Serra-Diaz et al., 2014), or contractions in their ranges (Schloss et al., 2012, HilleRisLambers et al., 2013). In particular, those with narrow niche breadth may be especially vulnerable to changing climates due to their often limited geographic range, low dispersal capacity, low reproductive output, and limited physiological tolerances (Broennimann et al., 2006, Schloss et al., 2012). Further complicating these stressors, surface-disturbing land uses (e.g., urbanization, transportation corridors, military training, agriculture, recreational activities, and energy development) have altered vast areas of terrestrial landscapes (Leu et al., 2008), fragmenting habitat and disrupting habitat corridors. This potentially restricts the ability of species to migrate to new areas (Wilson et al., 2010, Beltrán et al., 2014). The combination of these global, regional and often local stressors – in the form of climate and land use changes – can interact in unexpected ways to cause further reductions in species distributions (Mantyka-Pringle et al., 2015). These interactions have not been extensively explored for desert landscapes, especially those facing an increase in pressure from energy development.

Deserts of the southwestern United States are increasingly being recognized as having great potential for energy development given the abundant wind, solar and geothermal resources (NREL, 2013;

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Hernandez et al., 2015) and have vast expanses of public land. In recent years, federal public policy initiatives have mandated or encouraged the construction of utility scale renewable energy development (abbreviated hereafter as "energy development"). Consequently, infrastructure and energy development in the Mojave Desert have increased in recent years (Leu et al., 2008, Barrows and Allen, 2009, Lovich and Ennen, 2011). This region is home to many species of conservation concern that face increasing degradation, fragmentation, and outright losses of habitat due to growing energy infrastructure (Lovich and Ennen, 2011, Vandergast et al., 2013), invasive plants and fire (Brooks and Matchett, 2006), military training, and recreation (Berry and Aresco, 2014, DRECP, 2015).

The Mohave ground squirrel, *Xerospermophilus mohavensis* Merriam is endemic (Frank and McCoy, 1990) to the western Mojave Desert in California, USA (Best, 1995) and has one of the smallest distributions among North American ground squirrels, occupying an area of just 20,000 km^2 (Hoyt, 1972, Hall, 1981, Zeiner et al., 1988–1990). *X. mohavensis* is protected as a threatened species under the California Endangered Species Act (Fish and Game Code Section 2050) and was petitioned for listing under the federal Endangered Species Act in 2005, though the United States Fish and Wildlife Service decided that federal listing was not warranted at that time. Recent initiatives by the United States to reduce dependence on imported oil and reduce greenhouse gas emissions by pursuing solar, wind, and thermal power in the Mojave Desert have again raised concerns about the status of this species (Inman et al., 2013, DRECP, 2015). *X. mohavensis* has responded to historical changes in climate by migrating to their current range from southern refugia after the Last Glacial Maximum (Hafner and Yates, 1983), though current and future land use changes and the limited period of activity (Best, 1995) and dispersal ability of *X. mohavensis* raise concerns that a rapidly changing climate may challenge the persistence of this species. Recent research has shown that the ranges of small mammals at high elevations in California, USA, have decreased within the last century – likely due to climate change (Moritz et al., 2008). Others have predicted that the distributions of many rodent species in Texas, USA, will decrease to 60% of their current distributions under some climate change predictions (Cameron and Scheel, 2001). Although similar changes in climate may have occurred historically, broad landscape changes driven by recent human development may dramatically hinder some species' abilities to adapt to and disperse across a rapidly changing landscape (Schloss et al., 2012) resulting in precipitous range contractions and population declines.

Species distribution models (SDMs) have been widely adopted as tools for casting projections of habitat suitability under future climate scenarios (Franklin, 2010), and have been incorporated into many conservation planning strategies as tools to identify new future habitat or existing climate refugia for protection from land use changes (Jones et al., 2016). These models correlate a species' current distribution to environmental variables and infer habitat suitability at locations where a species' presence is unknown. SDMs incorporating mechanistic interactions between organisms, their environments, and fitness consequences are often referred to as 'niche' models, and are generally preferred over models devoid of physiological knowledge (Tracy et al., 2006, Buckley et al., 2010). Models ignoring these fundamental evolutionary processes may produce accurate representations of current geographic distributions, but can misrepresent relationships between current geographic distributions and future climates (Hijmans and Graham, 2006; Botkin et al., 2007, Williams and Jackson, 2007) or overestimate vulnerability to extinction (Schwartz, 2012). Moreover, while these models often predict substantial changes to habitat suitability under future conditions, few account for the ability (or inability) of species to relocate to new areas with suitable habitat (Bateman et al., 2013). Dispersal ability strongly influences the resilience of species to climate change – both through range shifts in response to shifting habitat suitability, and through increased gene flow between populations that can influence the rate of in situ adaptation to changing conditions (Bell and Gonzalez, 2011).

The work here builds on previous studies of *X. mohavensis* habitat and connectivity (Esque et al., 2013, Inman et al., 2013, Dilts et al., 2015) by forecasting habitat suitability under two climate scenarios across an expanded study area and by augmenting the previously developed SDM with a model of dispersal to account for potential *X. mohavensis* range expansion. Here we explore the ability of *X. mohavensis* to shift its range in response to changing climates from 2015 to 2080 and address alteration of habitat due to current land use through the use of scale factors reducing habitat suitability in areas affected by surface disturbance. Finally, we ask what impacts proposed energy development might have on future *X. mohavensis* habitat. The methods presented here can serve as a template for incorporating dispersal and land use when assessing the impacts of climate change on habitat.

2. Materials and methods

2.1. Study area

Our study area covered 131,059 km^2 of the Mojave Desert and Sierra Nevada mountains in California, including portions of Inyo, San Bernardino, Kern, and Los Angeles counties, and encompassed the entire known historical range of *X. mohavensis* (Zeiner et al., 1988–1990). This area is characterized by desert mountain ranges and plateaus separated by lower elevations with geomorphic features such as washes, outwash plains, dry lakebeds and basins, and is constrained by high elevations of the Sierra Nevada mountain range to the west. We expand the region used by Inman et al. (2013) to accommodate potential shifts in available habitat to the north and east, which were expected under future climate scenarios. Our study area included extremes in elevation, however 90% of the study area is below 2500 m. Regional precipitation ranges from 100 to 350 mm per year, with more rainfall occurring in the winter than in the summer (Hereford et al., 2004) and at higher elevations. Temperatures range from below 0 °C in the winter months to over 54 °C in the summer, with considerable daily and geographic variation (Turner, 1994).

2.2. SDM and environmental data

A previously developed SDM was chosen to represent current *X. mohavensis* habitat (Inman et al., 2013), and was used to forecast how future habitat may be altered under multiple climate change scenarios. This model, hereafter referred to as 'current conditions model' was developed with MaxEnt (version 3.3.3e, Phillips et al., 2006) at a spatial resolution of 1 km, and relied on 629 locality records of *X. mohavensis* from multiple sources including the California Natural Diversity Data Base (CNDDB), the Mojave Desert Ecosystem Program, as well as recent trapping and survey work in the region (P. Leitner and D. Delaney, unpublished data). Prior to use in the SDM, records were thinned to 1 per each 1 km^2 grid cell, and observations prior to 1975 were removed to minimize the effects of drastic land use changes, such as urbanization or agriculture. A bias file – realized as a density surface of all observations – was used to reduce the influence of biased sampling (Phillips and Dudik, 2008) and was created using a 4 km search radius from each cell. Environmental correlates of habitat suitability representing land surface characteristics and surface water balance were used in the current habitat model to describe the niche space of *X. mohavensis*, and were selected previously from a suite of model candidates derived from 14 environmental variables described by Inman et al. (2013). The current conditions model was selected from a suite of 86 candidate models with an information theoretic approach using a modified AICc score that was bias corrected for small sample sizes (Burnham and Anderson, 2002), and showed an Area Under the receiver operating

characteristic Curve score (AUC; Fielding and Bell, 1997) on independently withheld data of 0.888 (Inman et al., 2013).

Two of the variables – surface texture and surface albedo – represented the physical properties of the surface substrate, and depend on the geomorphic surface of the landscape. These variables were assumed to remain stable over the decadal timeframe considered here and were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD11A1 Land Surface Temperature 8-day Global 1 km and the MODIS MCD43B3 16-Day L3 Global 1 km Albedo data products acquired from the Terra (EOS AM) satellite. The two remaining variables, climatic water deficit and cumulative winter precipitation, were assumed to change under the two climatic scenarios, and were represented with data from the California Basin Characterization Model (Flint et al., 2013). Climatic water deficit is defined as potential evapotranspiration minus actual evapotranspiration, where potential evapotranspiration represents the total amount of water that can evaporate from the ground surface or be transpired by plants (considering influences of both precipitation and temperature), and was calculated using a modification of the Priestly-Taylor equation (Priestley and Taylor, 1972) as described in Flint et al. (2004) and Flint and Flint (2012). Winter precipitation and climatic water deficit were defined as the 30-year mean of the sum or mean of the winter months (Oct–April), at a 1 km cell resolution, respectively. These environmental variables precluded the use of finer spatial resolutions due to their limited availability at spatial resolutions finer than 1 km.

To forecast how climate may change over time, the Intergovernmental Panel on Climate Change (IPCC) Assessment Report 4 (AR4) outlined four emissions scenarios based on the potential for global change in economic and human population growth, population demographics, consumption of fossil and alternative fuels, and technological development (IPCC, 2001). These scenarios provide a set of greenhouse gas constraints under which General Circulation Models (GCMs) can derive projections of future climate conditions. Both climatic variables were derived from downscaled GCM predictions produced by the NOAA GFDL CM2.1 model (Delworth et al., 2006) for the A2 and B1 emissions scenarios (representing medium-high, and low emissions, respectively), and are described in Flint and Flint (2012) and Flint et al. (2013). The A2 emissions scenario is among the highest of the AR4 CO_2 emissions scenarios predicting increasing CO_2 emissions through the end of the century, and the NOAA GFDL CM2.1 model is among the warmest and driest predictions of the AR4 models for the U.S. southwest (Cayan et al., 2008). The GFDL model was chosen because of its ability to predict a realistic representation of California's recent historical climate (Delworth et al., 2006), including the strong seasonal precipitation and evapotranspiration cycles of the California desert region (Cayan et al., 2008, Gao et al., 2012). The GFDL CM2.1 model is generally more sensitive to slight variations in emissions scenarios and predicts warmer and drier climates than other GCMs reviewed by the IPCC AR4 (Cayan et al., 2008), and has been commonly used in climate change response studies to represent more extreme climate change predictions (e.g. Byrd et al., 2015, Thorne et al., 2015). While newer IPCC assessment reports and emission scenarios are available, we chose to use the AR4 scenarios because recent work has shown few differences between species distributions derived from the AR4 and IPCC fifth assessment report (Wright et al., 2015) and due to their relevance with existing planning initiatives (DRECP, 2015).

2.3. Land use disturbance

To account for alterations due to current land use, we used a land use impact scenario representing possible degradation of *X. mohavensis* habitat from roads, urban centers, and areas with extensive vegetation disturbance due to agriculture or cleared vegetation. These land uses are generally thought to be incompatible with *X. mohavensis*, and were used to reduce the habitat suitability score where they occurred. Few data are available to suggest quantitative relationships between anthropogenic influences and *X. mohavensis* habitat degradation, and therefore we selected the medium impact scenario described by Inman et al. (2013) to represent a moderate level of habitat degradation rather than known and tested relationships. The medium impact scenario was defined as the middle point between the high and low impact scenarios used by Inman et al. (2013). Scale factors from the medium impact scenario for each current land use were based on expert opinion from field observations of *X. mohavensis* behavior (Inman et al., 2013). Urban areas were derived from the National Land Cover Database (NLCD) 2006 Percent Developed Imperviousness layer (Xian et al., 2011), while major roads were extracted from U.S. Census Bureau Topologically Integrated Geographic Encoding and Referencing (TIGER) line files. Agriculture and cleared vegetation were identified using two different methods because digitized agriculture lands were not available for the entire study area. Within the areal extent of current habitat, a spatial layer was derived from remote sensing and image interpretation as described in Esque et al. (2013). Comparable layers depicting agricultural areas were obtained from the National Land Cover Database 2006 (Fry et al., 2011) for the larger study area. Current roads, urban areas, and agriculture/cleared vegetation were represented as binary spatial layers at a 1 km cell resolution, and assigned scale factors to effectively reduce habitat suitability where their influence occurred. Scale factors for urban areas, major roads, and agriculture/cleared vegetation were: 0.750, 0.250, and 0.750, respectively, and were used to reduce the habitat suitability value in impacted cells by subtracting the product of the habitat suitability score and the scale factor from the habitat suitability score.

2.4. Energy development

Predictions of future habitat incorporated scenarios of current and proposed energy development for California and Nevada, based on the Solar Energy Development Programmatic Environmental Impact Statement (BLM and DOE, 2012). Areas designated as transmission corridors under the California Desert Conservation Area Plan of 1980 (BLM, 1980), and the West-wide Designation of Energy Corridors (DOE and BLM, 2008) were also included. Additional energy development projects (such as wind and geothermal sites) and their associated spatial footprints were identified and provided by the Renewable Energy Project Manager for the California Desert BLM District Office (G. Miller, unpublished data) and Southern Nevada BLM District Office (G. Helseth, unpublished data). As with the land use impacts, scale factors were assigned to reduce habitat suitability where energy development may occur by subtracting the product of the habitat suitability score and the scale factor from the habitat suitability score. Scale factors for transmission corridors, wind energy development, and solar energy development were: 0.300, 0.300, and 0.875, respectively.

2.5. Accessible habitat

The current conditions model was used to project habitat suitability under the A2 and B1 climate scenarios annually for the years 2015 to 2080. We translated these projections of habitat suitability into predictions of *X. mohavensis* distributions by implementing two dispersal scenarios. The first, a data informed dispersal scenario, was motivated by evidence suggesting that current landscape patterns of genetic diversity reflect long-term connectivity across multiple generations beyond distances dispersed by juveniles and that *X. mohavensis* gene flow has historically been quite high across its range (Matocq et al. 2014). The second, a no-dispersal scenario, operated under the assumption that the ability of *X. mohavensis* to disperse under climate change may be restricted, predicated on a hypothesis that *X. mohavensis* may be unable to shift its range in response to climate change.

The former consisted of 100 simulations of annual dispersal from 2015 to 2080 to identify areas of suitable habitat under the two climate scenarios that could be occupied given known juvenile dispersal rates

and by considering land use disturbance from the medium impact scenario. We term these areas 'accessible habitat' and estimate them as raster cells where at least 50% of the 100 simulations resulted in potential occupancy by 2030 or 2080 (online Appendix *A*1 and Appendix A2). Potentially occupied cells at each yearly time step were identified from the probability that *X. mohavensis* could reach a cell (P_{reach}), conditioned on the probability that the cell was suitable habitat.

We conditioned P_{reach} on the probability that dispersing animals could stay each year by setting P_{reach} to 0 in cells where habitat suitability values (after land use disturbance scale factors were applied) were considered 'not habitat' and were below the 5th percentile of habitat suitability scores (0.295; Liu et al., 2005) from the current conditions model. If the habitat suitability value (after scale factors were applied) was above this threshold, P_{reach} was taken as a kernel density point estimate from the distribution of known yearly dispersal distances (Fig. 1A). These dispersal distances were computed from annual displacement distances of natal sites to hibernacula of 11 juveniles from 1995 to 1997 (Harris and Leitner, 2005), which ranged from 0 to 6.2 km $*$ year^{-1}, with a mean of 1.7 km $*$ year^{-1}. A Euclidean distance surface from the nearest potentially occupied cell of the previous year was used to obtain the kernel density point estimate of the probability that *X. mohavensis* could reach a given raster cell from its straight-line distance to the nearest previously occupied cell. Potentially occupied cells for the first year of each simulation were enumerated by selecting contiguous blocks of habitat (areas with suitability scores above the 0.295 threshold) from the current conditions model containing *X. mohavensis* observations. We added an additional constraint to P_{reach} to account for the cost of traveling through unsuitable habitat to reduce P_{reach} in areas separated from occupied areas by raster cells with low suitability habitat. P_{reach} was reduced proportionally by this cumulative cost function, calculated from a minimum cumulative cost surface, and defined as:

$$cost = \sum_{i=1}^{n}\left(1-\frac{1}{1+(e^{-H_i-0.3})15}\right) \quad (1)$$

where n is the number of cells traversed and H_i is the habitat suitability value at cell i after land use disturbance scale factors have been applied. This equation was motivated from the assumption that few differences, if any, would be apparent in dispersal patterns in areas with habitat suitability above 0.6 – since 90% of known *X. mohavensis* localities occurred in areas with habitat suitability above 0.60. We therefore set cost to be similar in these areas, while areas with suitability values below 0.6 were given increasing costs to meet the assumption that areas with low suitability habitat were increasingly unlikely to be traversed (Fig. 1B). To assess the impact of uncertainty in dispersal rates, we added yearly spatial stochasticity through the use of uniform random surfaces ranging from 0 to 1 to ensure that not all cells with high P_{reach} values were reachable at any given time step in each simulation. Only raster cells with a P_{reach} greater than the deviates surface were considered potentially occupied each year. In addition to accessible habitat (calculated as raster cells where at least 50% of 100 simulations resulted in potential occupancy by 2030 or 2080 under the A2 and B1 climate scenarios), we also enumerate areas where 5% and 95% of 100 simulations resulted in potential occupancy to investigate how uncertainty in dispersal rates may affect accessible habitat. This uncertainty is expressed as differences between accessible habitat and the areas where 5% and 95% of 100 simulations resulted in potential occupancy. The net change in total accessible habitat and the amount of new accessible habitat gained due to changes in climate is reported along with overlap between accessible habitat under the A2 and B1 climatic scenarios to identify co-occurring areas under the two differing climate scenarios.

The second dispersal scenario assumed no dispersal and was implemented using the same methods to estimate accessible habitat, with one exception: rather than using juvenile dispersal distances computed from annual displacement distances, we set dispersal distances to zero to assess the outcome if *X. mohavensis* was unable to shift populations into new unoccupied habitat. We report the amount of current habitat lost under the A2 and B1 climate scenarios for 2030 and 2080 under this dispersal scenario.

The degree to which accessible habitat may be affected by energy development was evaluated by including scale factors for energy development along with the scale factors for land use disturbance in a separate set of dispersal simulations, thereby creating an energy development scenario to assess potential effects of energy development on future *X. mohavensis* habitat. We report the total amount of habitat predicted under this energy development scenario for each of the climate scenarios. We also report the mean habitat suitability score (without energy development scale factors) in areas with proposed energy development and the mean of habitat suitability scores for the remainder of the study area to identify if areas with proposed energy development are predicted to have greater habitat suitability under either of the two climatic scenarios in 2080. We also identify areas of conservation concern where accessible habitat under the two climatic scenarios overlaps with areas where energy development is proposed.

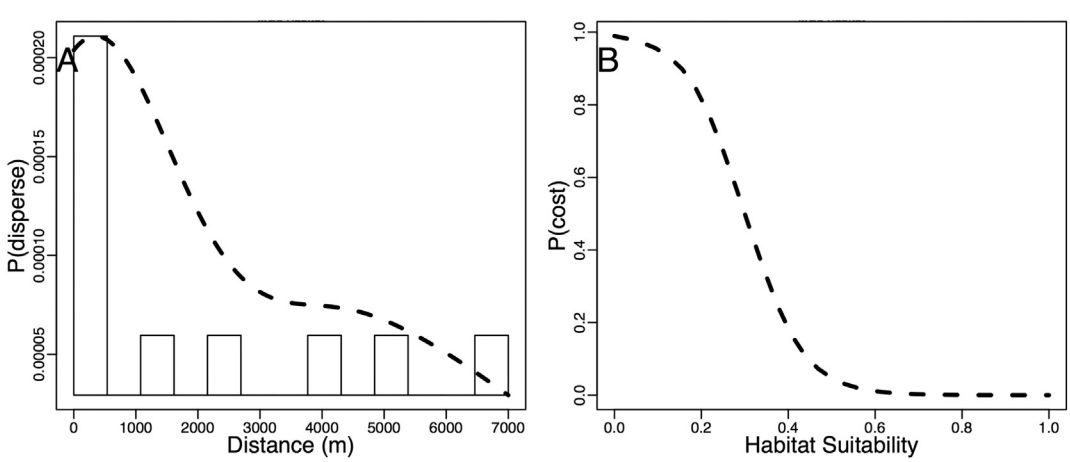

Fig. 1. Movement and colonization probability. A) Movement function applied to annual climate change migration functions derived from movement data for Mohave Ground Squirrel (Harris and Leitner, 2005). The probability of movement for a given distance is on the y-axis, and the potential distance moved in meters is on the x-axis. B) Cost function – derived from habitat suitability – for traversing to new habitat during annualized dispersal simulations to estimate potential responses of Mohave Ground Squirrels to climate change induced habitat shifts.

3. Results

3.1. Accessible habitat

Under the altered climate regimes predicted by the A2 and B1 climatic scenarios and the assumption of no dispersal, losses of 11.0% and 10.8% of extant habitat are predicted by 2030. When considering dispersal ability, gains of new accessible habitat may provide an additional 38.7% (Fig. 2) and 38.3% (Fig. 2) of habitat beyond current amounts for the A2 and B1 climatic scenarios, respectively (Table 1). This may result in an increase over the 12,721 km^2 of extant habitat under the A2 and B1 scenarios (Fig. 3; Table 1), though when uncertainty in dispersal estimates was considered, these increases could be offset by as much 6.3% and 8.5% for the A2 and B1 scenarios, respectively. Under the no dispersal scenario, losses of 52.7% and 64.0% of extant habitat by 2080 are predicted under the A2 and B1 climatic scenarios, respectively (Table 1). In contrast, allowing for dispersal suggested an increase in suitable habitat by 2080 of 37.0% and 49.8% for the two climatic scenarios, though uncertainty in dispersal estimates may alter these increases by 6.0% and 2.5% (Table 1).

Overlap in predictions of habitat between the climate scenarios was considerable, with 15,456 km^2 of habitat common under A2 and B1 predictions in 2030 (Fig. 4A). This overlap represented 90.8% of the 17,017 km^2 of total habitat predicted under either climatic scenario, suggesting high congruence between the two climatic scenarios early on. Non-overlapping habitat was limited to fringe areas along the periphery (Fig. 4A), with the majority of incongruent habitat being compressed at the base of the Sierra Nevada and San Bernardino Mountains escarpments. In contrast, by 2080, only 8584 km^2 (65.7%) of the 13,056 km^2 of habitat from both climatic scenario is shared between scenarios (Fig. 4B). Here, the majority of non-overlapping habitat from the B1 climatic scenario was located to the north, while the majority of non-overlapping habitat from the A2 climatic scenario was located to south and east, again along the fringes of the core habitat areas (Fig. 4B). Areas with overlapping new accessible habitat were constrained to the Owens Valley by the Sierra Nevada and White Mountain escarpments.

3.2. Energy development

Although the footprint for renewable development used here did not vary through time, the total area and configuration of habitat did, resulting in differing impacts for each of the two time periods. Thus, the predicted effect of energy development interacted strongly with climate scenarios. By 2030, the addition of energy development to the no dispersal scenario resulted in an additional loss of 436 km^2 and 423 km^2 of current habitat under the A2 and B1 climatic scenarios, respectively (Table 1). Combined with the climate scenarios, we predict losses of 1830 km^2 and 1793 km^2 of habitat identified in the current conditions model. When dispersal was considered, a net gain of 4708 km^2 and 4655 km^2 of habitat by 2030 under the A2 and B1 climatic scenarios was predicted (Table 1). By 2080, this pattern was nearly unchanged, with an additional reduction of 453 km^2 of habitat under the A2 climate scenario and renewable development, but only an additional 332 km^2 when renewable development scale factors were considered under the B1 climatic scenario.

Areas with proposed energy development showed 0.052 and 0.057 higher average habitat suitability scores than the rest of the study area for the A2 and B1 climatic scenarios in 2030, respectively. By 2080, the average habitat suitability values were only marginally higher in areas with proposed renewable development, with a 0.021 and 0.017 increase for the A2 and B1 climatic scenarios, respectively. While higher average suitability scores suggest that areas proposed for renewable development have higher suitability habitat than that found across the region, these differences are relatively small compared to the entire range of suitability values (0–1) predicted in the study area.

4. Discussion

Our study has found that the effects of a changing climate on *X. mohavensis* habitat suitability may be greater over the next 70 years than the effects of 2010 levels of proposed renewable energy development. Current habitat for *X. mohavensis* may be reduced by up to 52.7% by the year 2080 under the A2 emissions scenario, but shifts in accessible habitat may provide an offset of 6330 km^2 (49.8%) of habitat, resulting in a net loss of 1800 km^2 (14.1%). Losses under the B1 scenario were surprisingly similar despite this being a less severe scenario with respect to expected climate change. When cast in light of proposed energy development, an additional 453 km^2 of extant habitat may be affected under the A2 climatic scenario by 2080, though only an additional 332 km^2 under the B1 climatic scenario will be impacted by renewable energy. While we found considerable differences in *X. mohavensis* habitat between the two extreme emission scenarios, we also identified large regions of congruence by 2080 – both for habitat lost, and for new accessible habitat gained. Incorporating multiple emission scenarios in estimates of future habitat is critical for species distribution models intended for conservation planning due in large part to the wide range of climate uncertainty represented across different scenarios (Beaumont et al., 2008). Regions of congruence between the scenarios can help incorporate multiple estimates of future habitat into land use planning efforts as areas to prioritize for conservation. Likewise, sessile species and those with low dispersal abilities may not have the ability to shift or otherwise change their ranges to keep pace with climate change (Schloss et al., 2012), further complicating the prioritization of areas for conservation under changing climates.

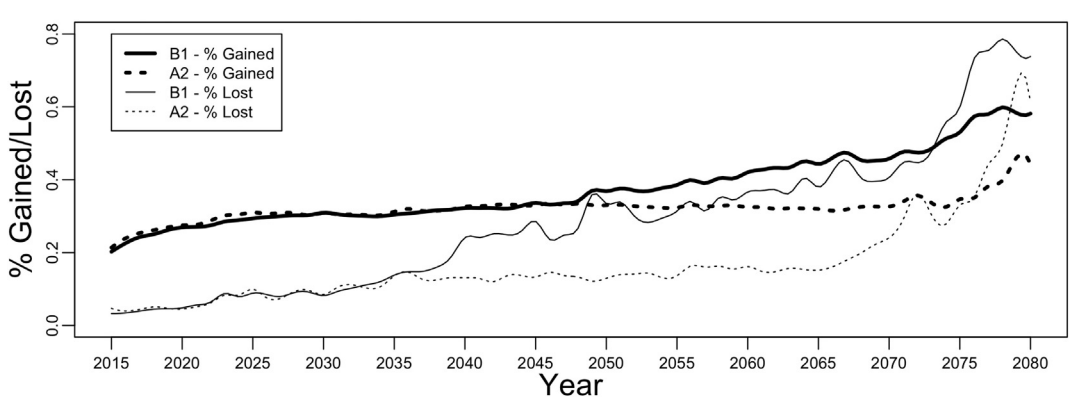

Fig. 2. Estimates of annual change in habitat area under the two climate forcing scenarios. Amount (km^2) of current habitat lost (thick) or new habitat gained (thin) each year under the B1 (dashed) and A2 (dotted) scenarios over the current conditions model.

Table 1
Accessible habitat totals (km^2) under the two climate scenarios (A2, B1) for two times steps (2030 and 2080) with and without proposed renewable energy. Area totals include No Change, Loss, Gain, and Gain Uncertainty and represent the total amount of accessible habitat that remained or was lost or gained relative to the current distribution by 2030 or 2080. Gain uncertainty was estimated by taking the difference in areas where 5% and 95% of 100 simulations resulted in potential occupancy. The amount of habitat remaining (No Change) plus the amount of habitat lost (Loss) equals the total amount of current habitat, while the amount of habitat remaining (No Change) plus the amount of habitat gained (Gain) equals the total amount of potential habitat under the given year and climate scenario.

Year	No energy development					Energy development			
	Total	No change	Loss	Gain	Gain uncertainty	Total	No change	Loss	Gain
A2 (km^2)									
Current	12,721					12,721			
2030	16,250	11,327	1394	4923	(+/−) 308	15,599	10,891	1830	4708
2080	10,718	6017	6704	4701	(+/−) 282	10,116	5564	7157	4552
B1 (km^2)									
Current	12,721					12,721			
2030	16,224	11,351	1370	4873	(+/−) 415	15,583	10,928	1793	4655
2080	10,922	4591	8129	6330	(+/−) 157	10,449	4259	8462	6191

4.1. Changing climate

Climate change poses new adaptive challenges to species persistence, but its influences are complicated by decisions about where human populations and their infrastructure will expand or contract (Mantyka-Pringle et al., 2015). This is especially true under a new energy future where alternative sources of energy are being developed in areas previously untouched by human activities (McDonald et al., 2009). In this rapidly changing environment, forecasting the potential futures of ecosystems and their inhabitants relies not only on an accurate understanding of how species are responding to changing climates, but also a strong understanding of their possible behavioral and physiological responses to altered land uses (e.g., solar or wind facilities). The latter is ever more important with the acceleration of alternative energy development, yet remains under studied and poorly understood (Northrup and Wittemyer, 2012).

While management decisions are often based on the "best available data", distribution models incorporating influences of a changing climate and altered land uses are all too frequently ignored in the decision process (Oliver et al., 2016), or are included using simplistic climate correlations absent of physiology or behavioral knowledge (Baldwin et al., 2014, Stephens et al., 2015). Models tied mechanistically to climate-space are far better suited for predicting the potential outcomes from climate change and should be included in management decisions where possible (Tracy et al., 2006). However, predictions of habitat shifts in response to global climate change cannot be based solely on analyses of climate-space changes, because species distributions are also governed by a complex array of biological factors including: reproduction, adaptation, and dispersal – interacting with suitable attributes of the physical environment. Similarly, changes in climate are not expected to be linear progressions (IPCC, 2001), and thus it is important to account for the succession of small annual changes in each of these factors rather than relying on a forecast of a single change some number of years into the future.

We use mechanistically relevant habitat variables in a presence-only SDM to create projections of future habitat and used annual dispersal simulations and current land-use degradation to forecast potential shifts in *X. mohavensis* distributions under two climate scenarios. Gains of new accessible habitat were initially similar between the scenarios, though they begin to diverge in 2039 with the A2 scenario gaining more new accessible habitat. This trend reverses in 2055, thereafter predicting greater habitat gains for B1 (Fig. 2). Generally, the B1 emissions storyline and scenario family is more optimistic than the A2 scenario, and we expected less habitat loss than under the A2 emissions storyline (IPCC, 2001). However, for our study area, winter precipitation was predicted to be higher in the B1 scenario until 2049, after which the B1 scenario showed lower precipitation than the *A*1 scenario (Fig. 5). In contrast, climatic water deficit shows a reversal of this pattern, with the A2 scenario predicting higher climatic water deficit than the B1 scenario up to 2033, but lower climatic water deficit thereafter (Fig. 5). These differences resulted in considerable departure between the two scenarios in terms of total habitat loss through 2080, though the amount of overlap between the two scenarios remained high: 90.8% in 2030 and 65.7% in 2080 (Fig. 4B). The differences between the two scenarios by 2080 were primarily attributable to the increase in newly accessible habitat in the B1 scenario.

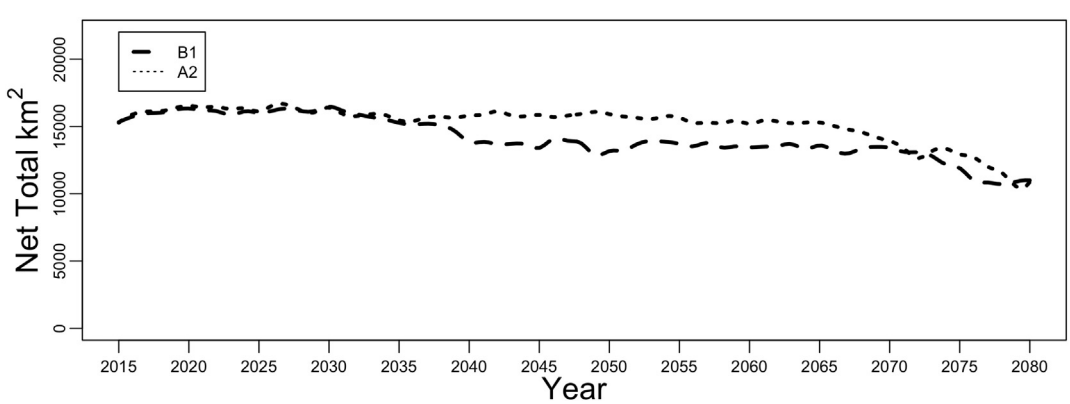

Fig. 3. Estimates of annual total habitat area under the two climate forcing scenarios. Amount (km^2) of net (current conditions –lost + gained) habitat each year under the B1 (dashed) and A2 (dotted) scenarios.

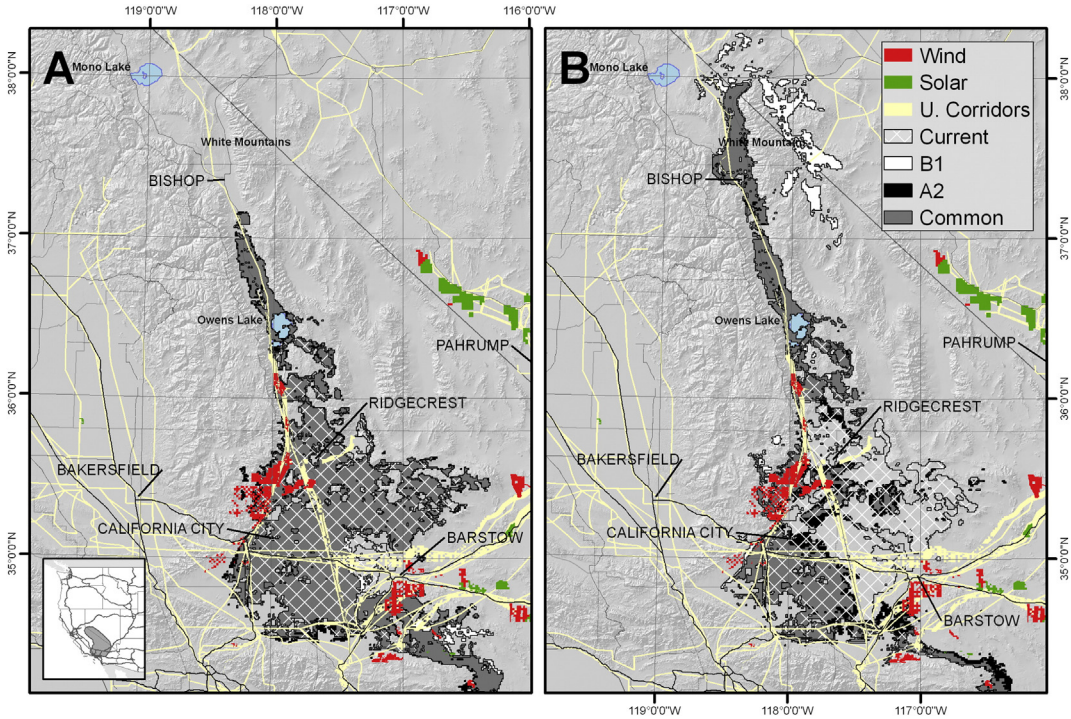

Fig. 4. Future accessible habitat and energy development. Accessible habitat under the B1 (white) and A2 (black) for the years 2030 (A) and 2080 (B). Areas of overlap between the two climate scenarios are shown in light grey. Accessible habitat was estimated with renewable development scale factors, and red areas indicate potential wind development areas, and green areas indicate potential solar development areas. Transmission corridors are highlighted in yellow. Large portions of current habitat (white hashed) may be lost by 2080 (B) under both climate scenarios.

By 2080, much of the new accessible habitat for *X. mohavensis* is predicted to be located in the Owens Valley, along US Highway 395. This relatively long and narrow valley is flanked by the Sierra Nevada, White Mountains, and stretches north from Owens Lake, CA, to beyond Bishop, CA into Nevada (Fig. 4B). No known efforts to sample for *X. mohavensis* have been made there, though the northernmost observation of *X. mohavensis* is on the southeastern edge of Owens Lake, suggesting that this valley may not be too dissimilar from current habitat. Overlap between the two climate scenarios was also substantial here (Fig. 4B), indicating a high likelihood that this area may become suitable for *X. mohavensis* occupancy in the future.

4.2. Renewable energies

While there is a general dearth of information on the effects of renewable energy on small fossorial mammal populations, recent work (Rabin et al., 2006) suggests that increased alert vocalizations and anti-predator vigilance behavior may occur in California ground squirrels (*Otospermophilus beecheyi*) from additional noise generated by the blades of wind turbine props. Little is known, however, about the cumulative impacts wind development facilities will have on the status of small mammal populations. Solar energy development likely presents a greater detriment to squirrel populations through the destruction

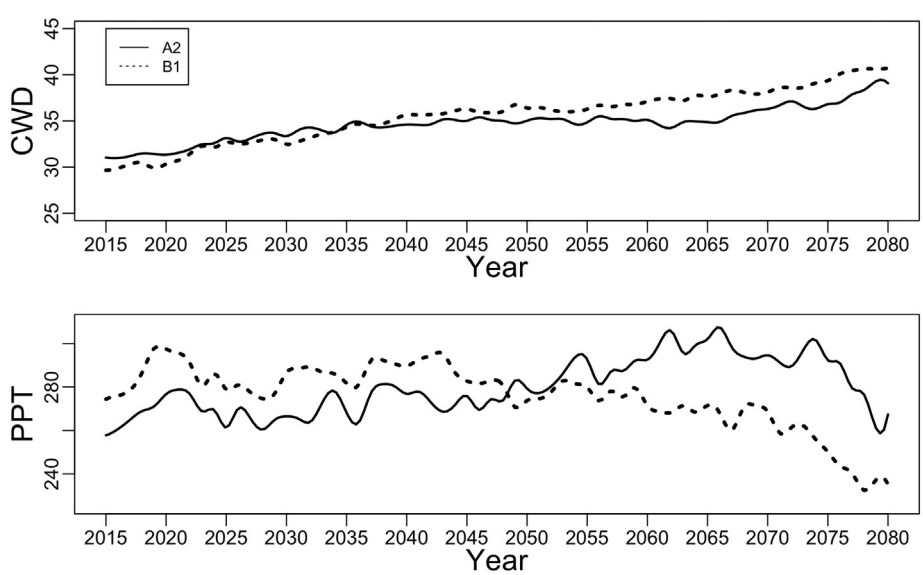

Fig. 5. Regional projections of climate covariates. Study area means of winter climatic water deficit (mm of H_2O) and winter precipitation (mm/year) for each year between 2015 and 2080 under the B1 (dashed) and A2 (solid) GFDL climate scenarios.

and direct modification of habitat, as well as indirect effects of increased roads, dust suppression and general habitat fragmentation (Lovich and Ennen, 2011, BLM, 2012). Similarly, transmission corridors are thought to have slight negative effects on many ground-dwelling species through the introduction of predators and exotic species (Stiles and Jones, 1998, Gelbard and Belnap, 2003), or altered vegetation communities (Clarke et al., 2006, King et al., 2009).

Our footprints of energy development used for these analyses were accurate as of October 2010, and represent a snapshot of proposed renewable development at that time. Due to continuous changes in applications and permits, best available data are continually replaced with updated energy development plans, and thus there is no definitive answer to exactly how much energy development will occur over the next century, or where that development will occur. Predicting the time and place of new renewable energy facilities spans the realms of renewable energy markets, infrastructure requirements and political climates, and is beyond the scope of the work presented here. When habitat degradation due to energy development was considered, additional losses of current habitat were observed – though were marginal relative to habitat lost due to projected changes in climate. Under the A2 climatic scenario, proposed energy development may affect 453 km^2 of habitat in addition to the 6704 km^2 of habitat that may be lost due to changes in climate by 2080. These estimates however, are highly conservative because only energy development on public lands was considered. Projects on private lands may cause additional loss of *X. mohavensis* habitat not considered here.

4.3. Assumptions, limitations and uncertainty

The estimates of accessible habitat presented here make a critical assumption that new accessible habitat will be not only be reachable by *X. mohavensis*, but will also be capable of sustaining populations for the years those areas remain suitable in the SDM forecasts. While this assumption is not entirely unreasonable, it needs to be explored further with field validation and translocation studies to better understand the ability of *X. mohavensis* to establish and maintain populations in new habitats. The scenario of dispersal used here also makes the assumption that *X. mohavensis* populations will move annually at rates found in the few known studies of juvenile natal dispersal. While we considered loss of habitat that may result from a no dispersal scenario, we were unable to incorporate effects that climate change may have on dispersal through temperature or other environmental changes. Altered temperature regimes may constrain spring and fall activity periods (Sharpe and Van Horne, 1999), thereby limiting periods where *X. mohavensis* may disperse – though the magnitude of these possible effects is unknown. In addition to impacts on behavior, our model of dispersal does not incorporate estimates of population vital rates or other demographic characteristics needed to estimate population viability, and therefore is an oversimplification of the mechanisms by which species' ranges shift. However, while the scenario of dispersal used here does not capture all of the intricate pathways that climate change may influence a population, we do include a scenario of no dispersal and incorporate yearly spatial stocasticity to capture uncertainty in dispersal estimates. This uncertainty was realized as error rates of up to 8.5% by 2030 and 6.0% by 2080, suggesting that the uncertainty in the future gains of habitat is substantially less than the magnitude of losses predicted under a no dispersal scenario (53% and 64% for the two climatic scenarios). This underscores the importance of putting estimates of future habitat in context of possible dispersal mechanisms: the future of *X. mohavensis* habitat may be influenced heavily on their ability to shift in response to changing climates.

Similarly, we did not incorporate specific estimates of soil condition (e.g., composition or structure) in the model because quality data describing dominant soil conditions are lacking for portions of *X. mohavensis* range. Instead of soil condition, we used a proxy for surface texture derived from thermal infrared spectroscopy relating dense rocky textures to areas with greater heat holding capacity. Fossorial organisms rely on friable soils, and our index of surface texture (see Inman et al., 2013 for methods) was derived to capture the variability in surface friability. Also absent were estimates of vegetation community structure under projections of climate change because specific plant species required for *X. mohavensis* populations are currently unknown and because projections of vegetation community projections under changing climates are meager at best. The condition and phenology of plants depend on weather conditions and environmental conditions among years (Recht, 1977), and vary with changing climatic conditions. These changes will be difficult to quantify for Mojave Desert species. Broadly speaking, *X. mohavensis* occupy vegetation communities in the high desert plains and hills throughout the western Mojave Desert. Examination of extant vegetation communities present within future accessible areas may provide insight to the types of communities that *X. mohavensis* may need to occupy under changing climates. There are three major vegetation types represented within these areas: high desert plains and hills, Owens' Valley vegetation, and shrub steppe vegetation (Barbour et al., 2007). While the Owen's Valley vegetation communities are different than those currently occupied by *X. mohavensis*, species important to *X. mohavensis* diets such as *Atriplex confertifolia* (shadscale), and *Kraschenninikovia lanata* (winterfat) are broadly present among them. Each of these species may also be found in shrub steppe habitats, but temperature regimes are cooler, and these species are far less dominant. Thus, shrub steppe habitat is least similar to areas presently occupied by *X. mohavensis* and may be most difficult to immigrate into. However, due to drastic changes in precipitation and climatic water deficit predicted under the two scenarios considered here, it is unlikely that vegetation communities will remain unchanged. Better predictions of future vegetation communities will undoubtedly improve SDMs and their forecasts of habitat suitability under altered climate regimes.

Climate change issues and research have been at the forefront of public interest and scientific investigations in recent years. The need for new tools to relate species responses to changes in climate has caused scientists to modify existing tools used for modeling habitat to incorporate forecasts of climate change into future predictions of habitat availability. However, while habitat models used in this manner provide useful quantitative predictions of habitat in a changing world, they are not without error, and should be interpreted as predictions made with assumptions and inherent error. Few methods exist to represent all of the uncertainty inherent in predictions of future habitat because of the many sources of error contained in each of the GCMs (Tebaldi et al., 2005, Collins et al., 2011), emissions scenarios (IPCC 2001), downscaled climate variables (Flint and Flint, 2012, Flint et al., 2013), and habitat models (Rocchini et al., 2011). In particular, the choice of methods in downscaling coarse GCM outputs into regional projections of climate needs to be considered in conservation studies (Harris et al., 2014). The uncertainty imparted in climate downscaling is often overlooked, and has been identified as a need for continued research (Salvi et al., 2015). For example, in preliminary work, we found considerable differences in projected climatic water deficit between regionally downscaled CMIP3 hydrologic projections (Reclamation, 2011) and the California Basin Characterization Model of downscaled hydrologic projections (Flint et al., 2013), but chose to use the later due to its prevalence in hydrologic modeling applications in California (e.g., Torregrosa et al. 2013, Chornesky et al., 2015).

The predictions of *X. mohavensis* habitat are based on the best available knowledge and data, but will undoubtedly be improved upon by future modeling as scientists continue to improve and refine global climate models, emissions scenarios and downscaling methods, and continue to refine our understanding of species' habitat requirements and inter-species interactions. Reduced uncertainty and improved utility will help future efforts to be more precise in deriving estimates of future habitat suitability.

4.4. Local conservation recommendations

As demand for sources of alternative energy increases, so too will the need for specific mitigation strategies to offset new environmental impacts. This work identified an area of current habitat (Fig. 4A) that is predicted to persist as habitat under both climatic scenarios, but is slated for wind energy development under current management plans. This area serves as an important corridor for gene flow among populations in the current distribution of *X. mohavensis* (Matocq et al., 2014, Dilts et al., 2015), and currently contains one of three distinct genetic groups within the species (Bell and Matocq, 2011). Under future climate regimes, this area may also serve as an important corridor of habitat to facilitate movement of individuals from areas that may become unsuitable.

5. Conclusions

Estimates of future habitat lacking dispersal considerations can drastically overestimate the amount of available habitat (Bateman et al., 2013), and may cause conservation planning efforts to incorporate unrealistic range shifts into habitat conservation plans. By incorporating dispersal-limited estimates of future habitat and detrimental land uses (e.g., roads, urban areas and agricultural/cleared vegetation) prior to assessing the effects of renewable energy, we provide a more appropriate measure of the amount of 'impacted' land due to renewable energy than would be assessed if climate-niche models had been used in absence of dispersal limitations and land degradation. Our use of scale factors to incorporate land degradation and dispersal scenarios provides a novel method for enumerating the assumed differences between multiple land use activities and for distinguishing accessible areas that may represent potential habitat from areas that are predicted to be 'suitable,' yet would be unavailable to squirrel populations due to dispersal limitations (i.e. inaccessible).

Resource managers charged with preserving biodiversity while managing for multiple uses of public lands face increasing demands and pressures with climate change and increased development of renewable energy. Tools for predicting the consequences of land use planning decisions (e.g., development of utility-scale renewable energy) on wildlife habitat in the context of climate change are ever more important for managers and policymakers. In particular, habitat models incorporating population demographic traits provide a greater degree of biological realism, and can give managers and policymakers greater insight to long-term ecological responses to land use decisions by incorporating aspects of population biology that are not often considered with species distribution models.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.05.033.

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